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Quantitative investigation of the area and volume in different compartments of the intestine of 18 mammalian species

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Abstract

Investigated the morphometric parameters of the small and large intestines of 18 mammalian species. A new method is described for morphometric study of intestines by means of planimetry using the entire intestine to calculate basal surface areas. In addition a computer-aided programme is presented for assessing surface enlargement of the intestinal mucosa at the light-microscopical level. The latter gives a surface enlargement factor which can be multiplied by the values gained from planimetry to give a final total surface enlargement of the intestine. The data are presented in coordinate systems and are used for calculating linear regression. The results show clearly that basal areas of small intestine, colon and total intestine scale almost isometrically to metabolic body weight, whilst caecum scales slightly negative allometrically. Areas of all intestinal compartments scale negative allometrically to absolute body weight. Volume shows positive allometric scaling to metabolic body weight and approximately isometry to absolute body weight (except for caecum: negative allometry).

The relation of area to volume in the form of ratios (area/volume) gives an estimate of the area available per unit volume. In this case smaller animals appear to have a more advantageous relationship of area to volume than large animals. This fact is interpreted as a correlate to the higher metabolic needs of smaller animals.

Introduction

It has long been recognized that size imparts profound consequences on structure and function in organisms and that food and size are interrelated (Schmidt-Nielsen 1975). The concept of scaling is concerned with the effects and consequences of changes in size. Isometry describes the situation where a change in any one linear dimension is accompanied by a change in all other linear dimensions in exactly the same proportion. Non-isometric scaling is termed allometry.

According to Kleiber's law (Kleiber 1961) basal metabolic rates scale to body mass in mammals with an exponent value of 0.75. It can be expected then that organs concerned directly with metabolic turnover also scale to body mass in accordance with this factor. Most obviously the acquisition and utilization of nutrition and the organ system involved in these processes (gastrointestinal tract) would fall into the category of these expectations. The development of homoiothermy and consequent high metabolic rates in mammals have been reviewed by Karasov and Diamond (1985) (see also Duncker 1989).

Certain generalities are obvious with respect to the appearance of the gut in extreme dietary forms, such that voluminous large intestines (caecum and/or colon) are most commonly found in herbivores (Grassé 1973; Parra 1978; Langer 1986, 1987a, b; Stevens 1988), whilst a shorter and more simply constructed large intestine is rather characteristic of faunivores (Chivers and Hladik 1980, 1984; Karasov and Diamond 1988). The occurrence as well as relative size of caecum and colon has been correlated to dietary adaptations (Ulyatt et al. 1975; Janis 1976; Hladik 1978; Hume and Warner 1980; Björnhag 1987; Langer 1987b; Chivers 1989; McBee 1989). In some species a caecum is missing altogether (Mitchell 1905; Gorgas 1967; Arvy 1972; Behmann

1973). The large group of animals which use a dietary adaptation intermediate between strict herbivory and faunivory are much less typical or uniform in their morphological characteristics. Moreover, a pliancy in the form of the intestinal tract and an adaptative ability to various ambient conditions makes a strict categorization difficult (Langer 1984; Green and Millar 1987; Karaso and Diamond 1988; Hofmann 1989). Despite these constraints a number of authors has attempted to develop a rough scheme for grouping animals based on various criteria (Chivers and Hladik 1980, 1984; Martin et al. 1985; Chivers 1989; see also Langer 1987b; Snipes 1991). Only the above-cited investigators, however, have used morphometry to quantify these criteria.

Although many of the characteristics of gut structure in a particular species may be so obvious as to lead one to the supposition that it belongs to a particular dietary group, the use of quantitative data can either support or negate these subjective inferences.

Thus, in the present study parameters of area and volume of the small and large intestines of 18 mammalian species were measured by use of modern morphometric techniques and the data subjected to allometric analysis.

Materials and methods

18 different mammalian species (three animals per species with either one female and two males or two females and one male) were used in the present study. They were chosen according to two main criteria. One criterion used was to choose taxonomically closely related species (in order to keep the taxonomic influences at a low level), who differed substantially in body weight. Another criterion was to choose different species employing various dietary adaptations (e.g., faunivory, herbivory and intermediate forms as well as rumination). An attempt was made to handle all animals as similarly as possible in order to reduce the influence of this factor on the quantitative results. Due to the difference in availability of some animals from such sources as diverse as the laboratory or abattoir or the field this was not always possible. Table 1 is a listing of all animal species used in the present study.

In most cases fixation of the intestine was performed according to Fenwick and Kruckenberg (1987) via intraluminal filling. In small mammals segments of the gut used for light microscopy were very gently injected with Lillie's buffered formol avoiding distension of the lumen. The gut (duodenum to rectum) was opened lengthwise. From selected areas (see Fig. 1) 0.8 mm diameter

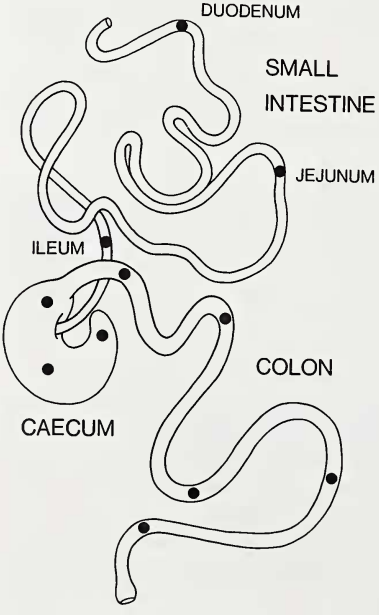

Fig. 1. Sampling for imagine analysis. Schematic drawing of the small and large intestines including caecum of an idealised intestine of a mammal. Black circles indicate sites of sampling. Diameters of 0.8 mm were punched out after the intestine had been opened lengthwise. For small intestine the sample for duodenum was taken within the first few cm of the start of the small intestine; ileum was taken a few cm orad to the ileocaecal junction. Jejunum was selected as being equidistant between these two points. The caecum was sampled in three areas: apex, corpus and near the caecocolical junction. The colon was divided into five equidistant segments from caecocolical junction to rectum. Within each of these segments a sample was taken

samples were punched out with a cork borer and placed immediately in Bouin's fluid and processed according to conventional methods for paraffin histology. Directly after sampling, appropriate lengths were sequentially flattened gently between two glass plates. The contours of the flattened gut were outlined immediately onto transparent paper and then areas of the contours were measured by means of a planimeter (in mm^2) (MOP, Kontron, Munich, FRG). The sum of these measured outlines for caecum and colon are termed BASAL AREAS.

By use of this method the disadvantages of sampling and extrapolation from measured samples to total lengths were avoided. Only in the case of the small intestine a 10-cm long segment (and not the entire small intestine) was excised and opened lengthwise. It was then flattened between the glass plates and subsequently the contours outlined. From this measured segment the entire area of the small intestine in mm^2 was calculated by multiplying this value times the total length of small intestine (Pénzes and Skála 1977).

The values of basal areas represent the means of three individual measurements of each outlined contour. A final mean was then calculated from the measurements gained from the three individuals of each species, which was then used for further statistical analysis. The various regions within the caecum or colon as depicted in Fig. 1 were not analysed separately in the present study, but rather were pooled to give one mean value for a species for caecum, for colon and for small intestine.

To access the increase in surface areas over and beyond this basal area, i.e., due to microscopically visible villi, crypts, mounds, plicae etc., the samples taken for light microscopy as described above and illustrated in Fig. 1 were subjected to analysis using a newly designed imagine analysing programme (IBAS, Kontron). The device consisted of a host computer and an image processing cabinet. The host computer controlled the system, assisted both interactive and automatic image analysis and performed the basic treatment of the data measured. A TV camera (VIDICON, Bosch, Stuttgart, FRG), mounted on a light microscope (UNIVERSAL, Zeiss, Oberkochen, FRG) was interfaced to the image-processing cabinet of the system. Images of the tissues were obtained using a 16× magnifying lens, stored in video memory after digitization and processed with a special processor included in the system.

The image analysing programme was developed to facilitate an automatic length measurement of both the flat tissue basal boundary and the corresponding folded surface boundary (i.e., the surface mucosal relief). Consequently, two values per individual field of view were measured. The programme included 1. image preprocessing to correct artifacts and to increase the overall contrast, 2. segmentation of the tissue from the background, and 3. identification and measurement of contour lengths. The programme was embedded into an easy-to-operate loop structure with interactive pauses for control and correction via mouse and digitizer tablet. After completion of a fixed number of measurements per specimen the scaled measurement values were stored permanently on harddisk. Accessing these values with a programme written in FORTRAN allowed to calculate a Surface Enlargement Factor (SEF) at the microscopical level by dividing the length of the folded surface boundary produced by the second-order (i.e. micro-anatomical) enlargements of the mucosa by the flat basal boundary (Fig. 2). This factor multiplied by the value obtained by planimetry (BASAL AREA) gives the final value of TOTAL AREA. Light-microscopical material from only 11 of the 18 species was available for determination of SEF values, as indicated in Table 1 with an asterisk.

Before routine measurement with this programme a pilot experiment was performed to standarize the number of sections (Zilles et al. 1982) and the number of measurements necessary for a statistically significant study according to the method of Baur (1969) which states that the sample size should never be less than twice the relative standard deviation of the samples, expressed as percentage. Volumes were calculated from measured parameters of length and basal areas according to the formula: $V = (\text{Basal area})^2 / 4 \times l$. All data were subjected to statistical analysis, primarily using linear regression curves with the help of Statgraphic and Harvard Graphics computer programmes. The values of the coefficients of correlation gave significance at the 0.1 % level.

Results

Table 1 is a compilation of the morphometric values gained in this study. Basal areas (measured by planimetry of flattened segments of gut) for each species are given in cm^2. Percentages of these values to the values for total intestine are also given. Surface enlargement factor (SEF) indicates the values measured by imagine analysis of histological sections. This factor multiplied by the basal area gives total areas which are also presented in Table 1 as cm^2 and percentages. Volumes are presented as ml and percentage of total intestinal volume. In the following account the term "total intestine" means additive values from small intestine, caecum and colon. Whenever the term "large intestine" appears both caecum and colon are considered together.

Table 1. **Empiricle values of the parameters of area and volume for small and large intestines of the 18 mammalian species used in the present study**
Basal areas were measured by planimetry and are given in cm^2 (below each value is the percent for this intestinal compartment to the total intestinal value). SEF is the surface enlargement factor gained by imagine analysis on histological sections. Total areas are products of basal area × SEF and are given in cm^2 and in percentages. Volumes are calculated values and are presented in ml and percentage of total volume of small and large intestine together

Species	Basal area (cm^2)				SEF			Total area (cm^2)				Volume (ml)			
	Small int	Caecum	Colon	Total	Small int	Caecum	Colon	Small int	Caecum	Colon	Total	Small int	Caecum	Colon	Total
Vole[a]															
Microtus agrestis	15.7	6.9	8.0	30.6	3.95	1.77	1.96	61.9	12.3	15.7	89.9	1.2	0.8	0.4	2.4
Body Wt 33.6 g	51.2 %	22.6 %	26.2 %					68.8 %	13.7 %	17.5 %		50.5 %	32.4 %	17.3 %	
Dwarf hamster[a]															
Phodopus sungorus	26.3	7.9	12.6	46.8	2.65	1.55	1.30	69.9	12.3	16.5	98.7	2.4	1.3	0.9	4.6
Body Wt 36.1 g	56.2 %	16.9 %	26.9 %					70.9 %	12.5 %	16.7 %		52.4 %	27.1 %	20.5 %	
Mouse[a]															
Mus musculus	46.1	8.6	13.1	67.8	2.56	1.81	1.57	118.3	15.5	20.6	154.4	4.6	1.7	1.6	7.9
Body Wt 47.5 g	68.0 %	12.6 %	19.3 %					76.6 %	10.1 %	13.4 %		58.3 %	21.5 %	20.2 %	
Gerbil[a]															
Meriones unguiculatus	34.3	11.3	12.3	57.9	2.55	1.75	1.66	87.7	19.7	20.6	128.0	3.6	2.7	0.9	7.2
Body Wt 81.3 g	59.3 %	19.5 %	21.3 %					68.5 %	15.4 %	16.1 %		50.1 %	37.1 %	12.7 %	
Mole rat															
Spalax ehrenbergi	30.6	30.8	14.3	75.7	–	1.55	1.50	–	47.7	29.8		2.9	3.2	0.9	7.0
Body Wt 122.5 g	40.4 %	40.7 %	18.9 %									41.4 %	45.7 %	12.9 %	
Golden hamster[a]															
Mesocricetus auratus	75.4	35.3	48.3	159.0	3.86	1.68	1.30	291.9	59.7	63.5	415.1	11.5	8.9	5.4	25.8
Body Wt 155.8 g	47.4 %	22.2 %	30.5 %					70.3 %	14.4 %	15.3 %		44.5 %	34.6 %	20.9 %	
Rat[a]															
Rattus norvegicus	113.4	26.6	22.2	162.2	2.26	1.55	1.66	257.3	41.2	36.8	335.3	11.4	8.9	2.7	23.0
Body Wt 298.0 g	69.9 %	16.4 %	13.7 %					76.7 %	12.3 %	11.0 %		49.6 %	38.7 %	11.7 %	
Muskrat[a]															
Ondatra zibethicus	203.6	165.3	127.1	496.0	2.80	2.52	2.11	571.2	417.1	269.1	1257.4	44.0	98.2	22.6	164.8
Body Wt 843.3 g	41.0 %	33.3 %	25.6 %					45.4 %	33.2 %	21.4		26.7 %	59.5 %	13.7 %	
Guinea pig[a]															
Cavia aperea	298.9	174.1	193.4	666.4	3.21	2.24	1.56	961.4	391.0	303.0	1655.4	51.9	135.2	29.3	216.4
Body Wt 979.4 g	44.9 %	26.1 %	29.0 %					58.1 %	23.6 %	18.3 %		24.0 %	62.5 %	13.5 %	

Rabbit[a]															
Oryctolagus cuniculus	442.2	512.5	268.1	1222.8	3.50	2.18	1.80	1548.1	1121.1	485.2	3154.4	79.3	514.2	50.1	643.6
Body Wt 357.9 g	36.2 %	41.9 %	21.9 %					49.1 %	35.5 %	15.4 %		12.3 %	79.9 %	7.8 %	
Nutria[a]															
Myocastor coypus	1040.1	362.1	312.7	1714.9	3.71	1.81	2.09	3865.7	655.9	654.5	5176.1	254.9	279.5	84.7	619.1
Body Wt 6316.7 g	60.7 %	21.1 %	18.2 %					74.7 %	12.7 %	12.6 %		41.2 %	45.2 %	13.7 %	
Dog															
Canis lupus	1124.8	57.7	251.6	1434.1	–	–	–	–	–	–	–	373.0	34.5	120.0	527.5
Body Wt 13,750 g	78.4 %	3.9 %	17.5 %									70.7 %	6.5 %	22.7 %	
Sheep															
Ovis ammon	6377.4	298.9	2433.6	9109.9	–	–	–	–	–	–	–	1503.2	284.4	766.5	2554.1
Body Wt 42,500 g	70.0 %	3.3 %	26.7 %									58.9 %	11.1 %	30.0 %	
Goat															
Capra aegagrus	3770.3	192.6	1341.2	5304.1	–	–	–	–	–	–	–	1187.0	140.6	340.9	1668.5
Body Wt 52,500 g	71.1 %	3.6 %	25.3 %									71.1 %	8.4 %	20.4 %	
Human[a]															
Homo sapiens	8044.8	145.6	710.5	8900.9	3.66	1.79	2.483	29512.4	261.7	1764.9	31539.0	14524.2	176.6	453.2	15154.0
Body Wt 86,660 g	90.4 %	1.6 %	8.0 %					93.6 %	0.8 %	5.6 %		95.8 %	1.2 %	3.0 %	
Pig															
Sus scrofa	10047.3	447.0	5405.3	15899.6	–	–	–	–	–	–	–	4406.6	564.8	3808.1	8779.5
Body Wt 111,850 g	63.0 %	3.0 %	34.0 %									50.2 %	6.4 %	43.4 %	
Cow															
Bos primigenius	27393.5	783.8	7426.9	35604.2	–	–	–	–	–	–	–	14662.8	857.7	4598.8	20119.3
Body Wt 474,300 g	76.9 %	2.2 %	20.9 %									72.9 %	4.3 %	22.9 %	
Horse															
Equus przewalskii	42183.4	9195.4	27928.1	79306.9	–	–	–	–	–	–	–	46897.3	56083.0	83892.7	186873.0
Body Wt 520,000 g	53.2 %	11.6 %	35.2 %									25.1 %	30.0 %	44.9 %	

[a] Material available from these species for both Basal areas and Total areas.

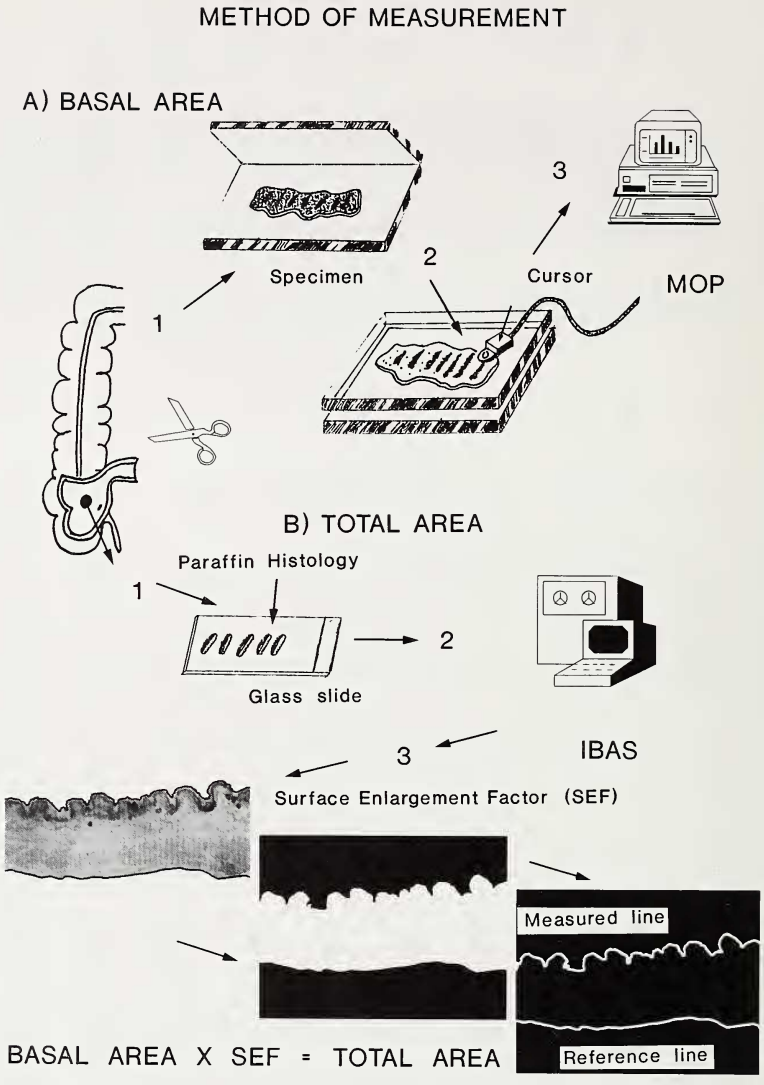

Fig. 2. Pictorial representation of the method of measurement (modified after Snipes 1991). A) Basal areas are obtained by opening the intestines lengthwise and taking appropriately long specimens (1) and flattening them between glass plates (2). A transparent paper is used to trace the outlines which are then measured with a cursor attached to the semi-automatic planimeter MOP (3). For Total areas (B) a 0.8 mm specimen is punched out of the intestine (1) (see Fig. 1 for sampling scheme) and processed for light microscopy. Sections (2) are analysed with the use of the IBAS imagine analysor to give a factor of surface enlargement (SEF) (3). The pictures at the bottom give three steps in the production of an image for measuring. At far right, the SEF value results from the measured line in relation to the reference line. Total area is the product of basal area and SEF

Areas

The calculated regression lines of the basal areas for all 18 species versus metabolic body weight are given in Fig. 3a–d. Small intestine (Fig. 3a), colon (Fig. 3c) and total intestine (Fig. 3d) scale close to isometry with respect to metabolic body weight. In all three cases the coefficients of correlation are significant at the 0.1 % level [small intestine: slope 1.01 ($r = 0.99$); colon: slope 0.95 ($r = 0.94$) and total intestine: slope 0.96 ($r = 0.99$)]. The data for caeca scale negative allometrically (slope 0.68; $r = 0.89$). Plotted against absolute body weight instead of metabolic body weight, the slopes for all intestinal regions fall to negative allometry (graphs not shown) (small intestine: slope 0.76; colon: slope 0.71; total intestine: slope 0.72 and caecum: slope 0.51). Correlation coefficients are all significant at the 0.1 % level.

Fig. 4a–d present the respective graphs for total areas (i.e. basal area × SEF) for the 11 species noted with an asterisk in Table 1. In these cases small intestine and total intestine scale isometrically with metabolic body weight (slopes 1.01 and 1.00, respectively); caecum and colon negative allometrically (slopes 0.77 and 0.89, respectively). Scaled to absolute body weight all values are much decreased (small intestine: slope 0.76; caecum: 0.57; colon: 0.66; and total intestine: 0.71).

Volumes

Calculated volumes for small intestine, colon and total intestine all scale positive allometrically with metabolic body weight (slopes, respectively, 1.33; 1.35; 1.30) (Fig. 5). Caecum is almost isometric (slope 1.03) (Fig. 5b). All "r" values are significant at the 0.1 % level. Plotted against absolute body weight these values do not decrease to negative allometry as was the case with areas, except for caecum, showing the most dramatic decrease (slopes: small intestine 0.99; caecum 0.77; colon 1.01; and total intestine 0.97) (graphs not shown).

Table 2. **Coefficient of gut differentiation**

Represents the ratio of the area of the large intestine divided by the area of the small intestine

	Basal area		Total area	
Human	11	(F)	7	(F)
Dog	27	(F)	–	
Cow	3	(R)	–	
Goat	41	(R)	–	
Sheep	43	(R)	–	
Rat	43	(I)	30	(I)
Mouse	47	(I)	31	(I)
Pig	58	(I)	–	
Nutria	65	(I)	34	(I)
Gerbil	68	(I–H)	46	(I)
Dwarf hamster	78	(H)	41	(I)
Horse	88	(H)	–	
Vole	95	(H)	45	(I)
Golden hamster	111	(H)	42	(I)
Guinea pig	123	(H)	72	(H)
Muskrat	144	(H)	120	(H)
Mole rat	147	(H)	–	
Rabbit	177	(H)	104	(H)

Large intestine = Caecum + Colon; all values × 100.

Rating: F = Faunivore: 0 – 30
I = Intermediate: 30 – 70
H = Herbivore: 70 +
R = Ruminant

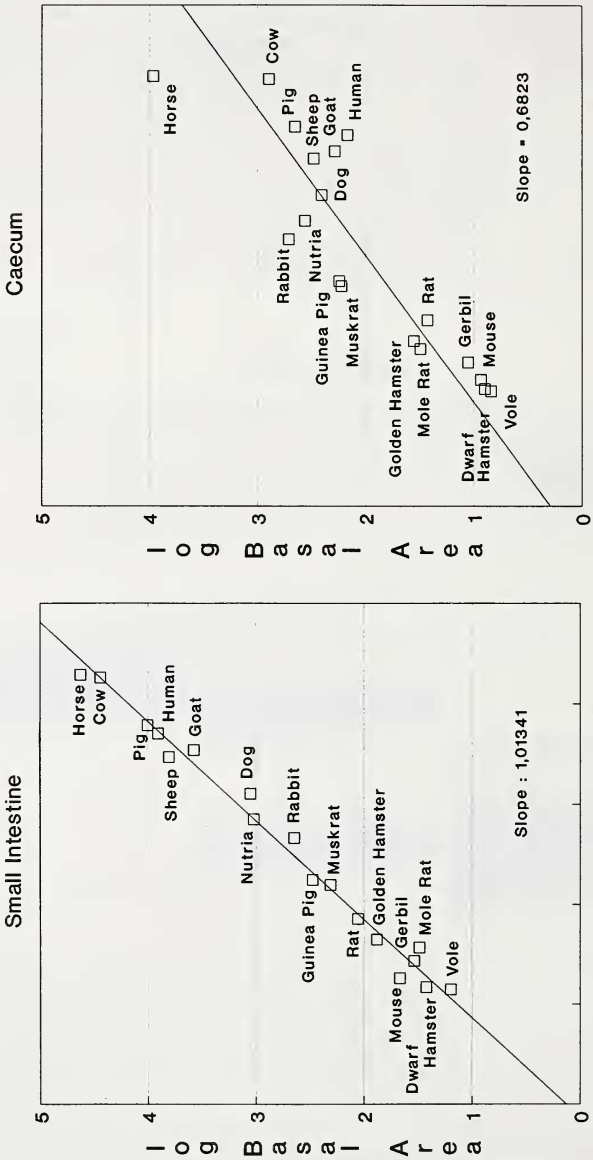
Small Intestine
log Basal Area
log Metabolic Body Wt
Horse
Cow
Pig
Human
Sheep
Goat
Nutria
Dog
Rabbit
Guinea Pig
Muskrat
Rat
Golden Hamster
Mouse
Gerbil
Dwarf Hamster
Mole Rat
Vole
Slope : 1,01341
Caecum
log Basal Area
log Metabolic Body Wt
Horse
Cow
Pig
Sheep
Goat
Human
Dog
Rabbit
Nutria
Guinea Pig
Muskrat
Golden Hamster
Mole Rat
Rat
Gerbil
Mouse
Dwarf Hamster
Vole
Slope = 0,6823

Fig. 3a

Fig. 3b

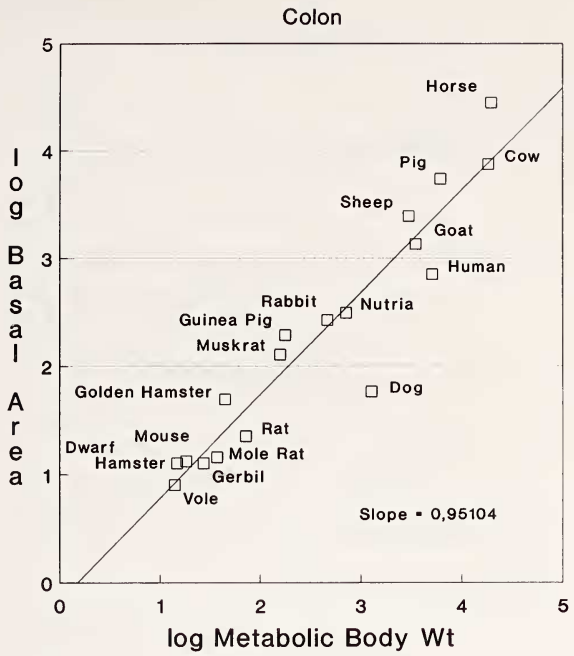

Fig. 3c

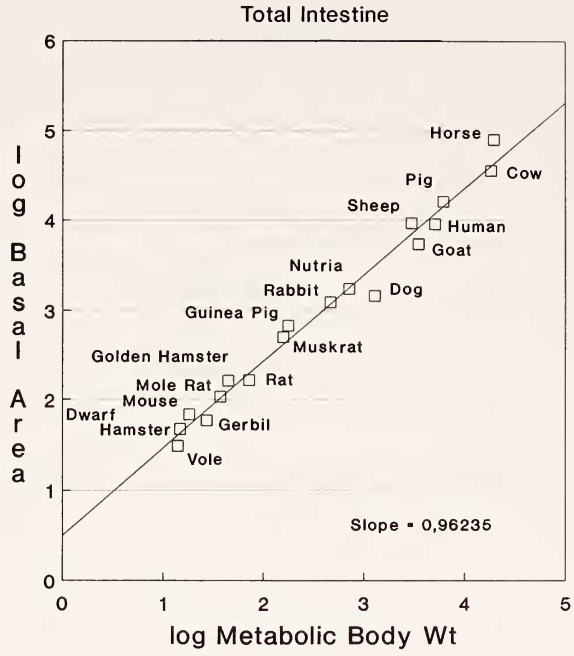

Fig. 3d

Fig. 3. Regression lines for basal areas (ordinate log cm^2) versus metabolic body weight (abscissa log grams). Slopes for the small intestine (3a), caecum (3b), colon (3c) and total intestine (3d) for the 18 animals were all significant by use of the coefficient of correlation at the 0.1 % level

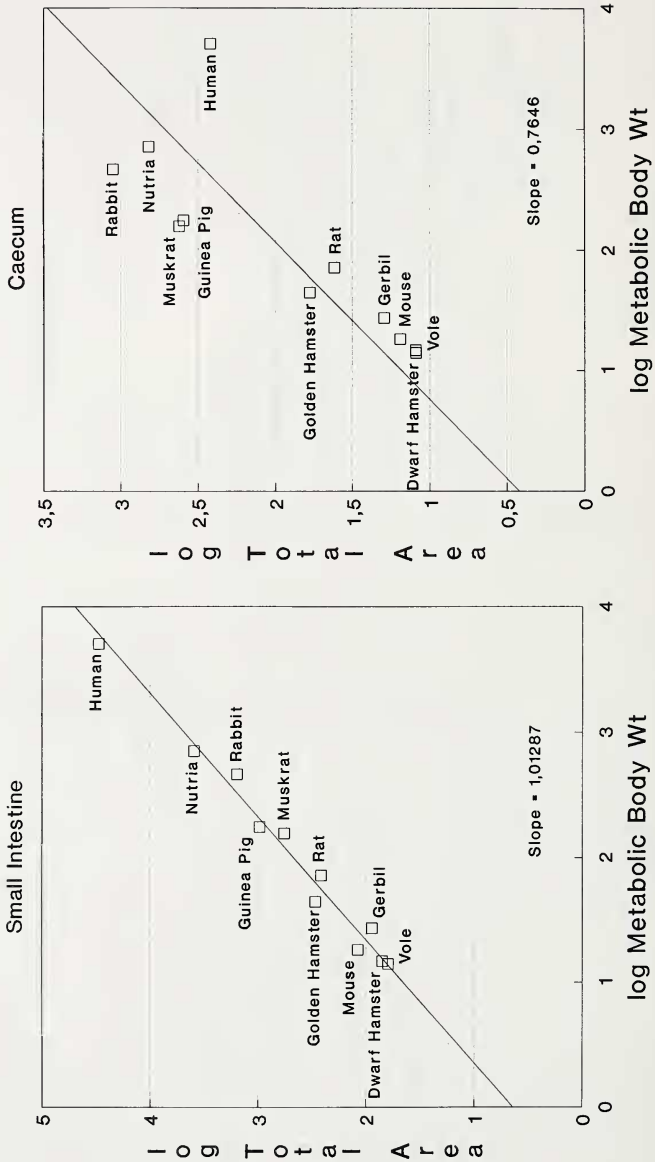
Small Intestine
log Total Area
log Metabolic Body Wt
Human
Nutria
Rabbit
Guinea Pig
Muskrat
Golden Hamster
Rat
Mouse
Gerbil
Dwarf Hamster
Vole
Slope = 1,01287
Caecum
log Total Area
log Metabolic Body Wt
Rabbit
Nutria
Muskrat
Guinea Pig
Human
Golden Hamster
Rat
Gerbil
Mouse
Dwarf Hamster
Vole
Slope = 0,7646

Fig. 4a

Fig. 4b

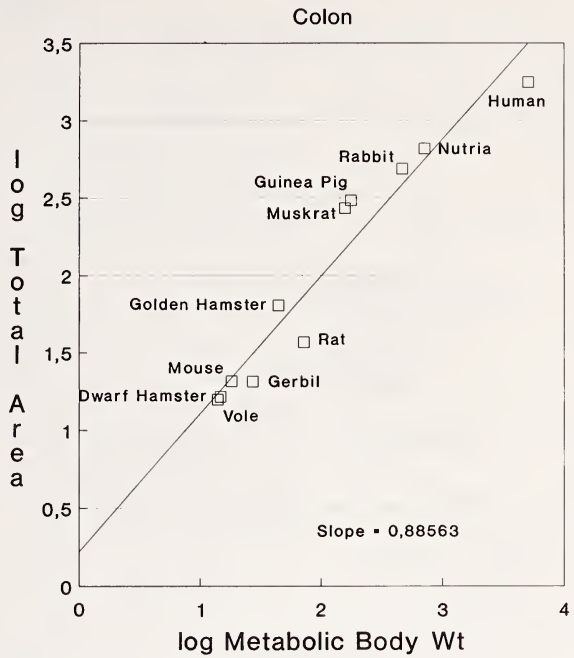

Fig. 4c

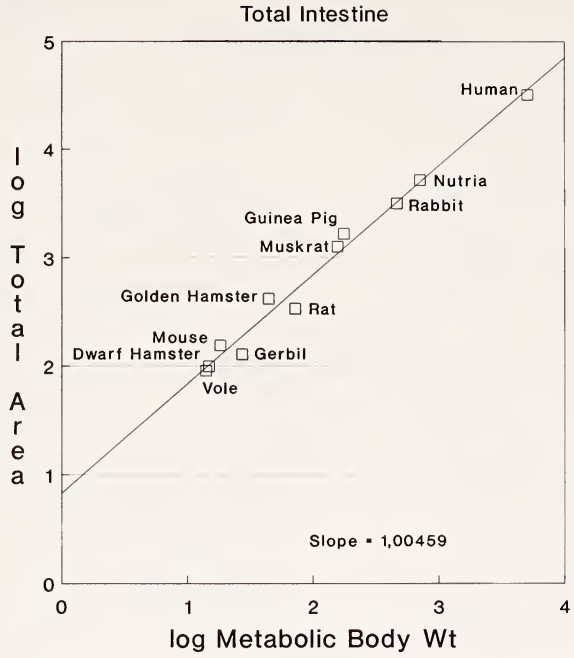

Fig. 4d

Fig. 4. Regression lines for total areas (basal area × SEF log cm^2) (ordinate) versus metabolic body weight (abscissa log grams). 4a: small intestine, 4b: caecum, 4c: colon, 4d: total intestine. The coefficients of correlation are significant at the 0.1 % level

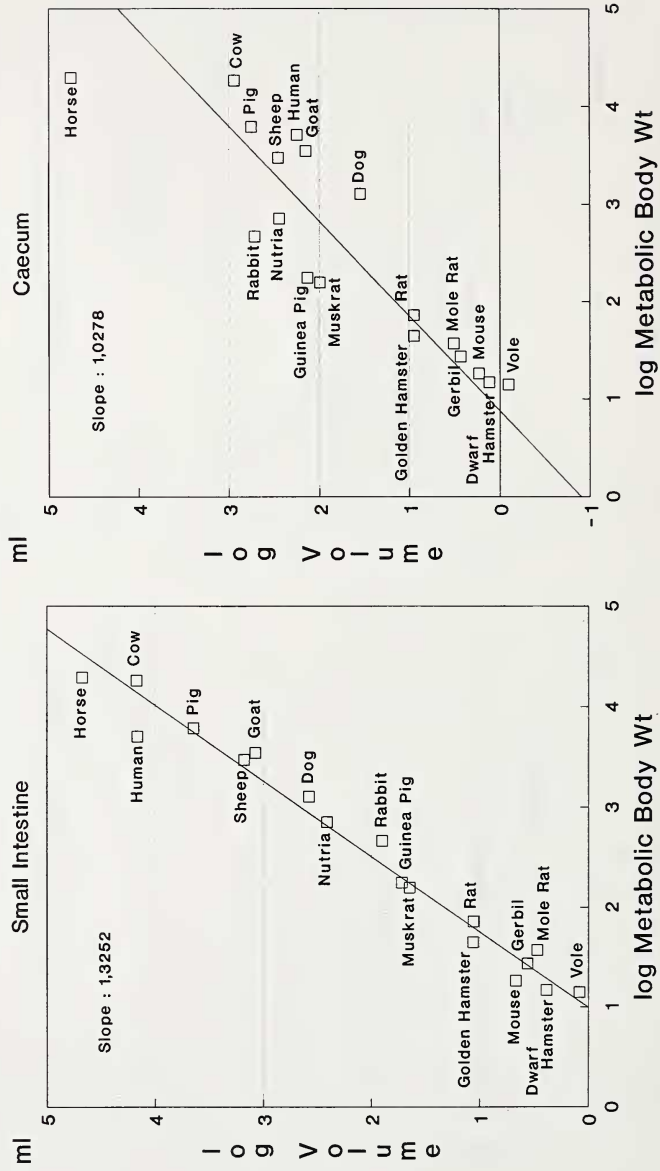
Small Intestine
ml
log Volume
log Metabolic Body Wt
Slope : 1,3252
Horse
Human
Cow
Pig
Sheep
Goat
Dog
Nutria
Rabbit
Guinea Pig
Muskrat
Rat
Golden Hamster
Gerbil
Mouse
Mole Rat
Dwarf Hamster
Vole
Caecum
ml
log Volume
log Metabolic Body Wt
Slope : 1,0278
Horse
Cow
Pig
Sheep
Human
Goat
Dog
Rabbit
Nutria
Guinea Pig
Muskrat
Rat
Golden Hamster
Mole Rat
Gerbil
Mouse
Dwarf Hamster
Vole

Fig. 5a *Fig. 5b*

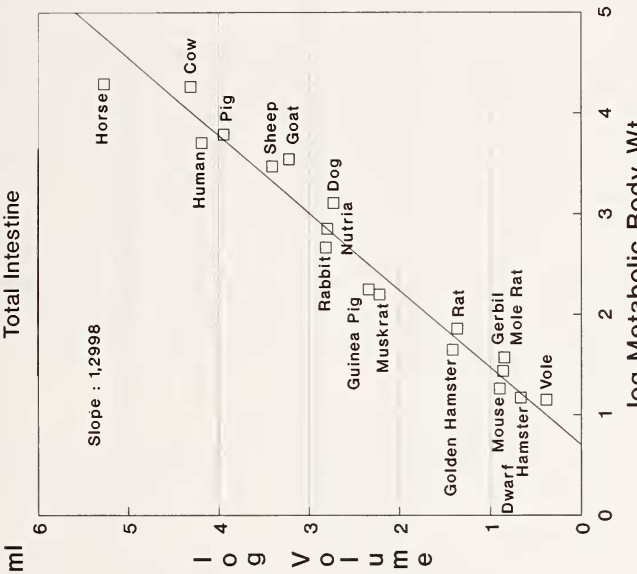

Fig. 5c

Fig. 5d

Fig. 5. Regression lines for volumes (ordinate log ml) versus metabolic body weight (abscissa log grams). 5a: small intestine, 5b: caecum, 5c: colon, 5d: total intestine. Note positive allometry. Coefficients of correlation all significant at the 0.1 % level for this parameter

Coefficients

A convenient method to visualize the area relationships of various animals and to attempt a classification based on the parameter of area is to calculate the "Coefficient of Gut Differentiation" (according to Chivers and Hladik 1980, 1984). This factor results from the ratio area large intestine/area small intestine. In this case large intestine includes the sum of caecum and colon. In Table 2 these values are given (× 100) for both basal areas and total areas. Based on similar values suggested by the above-mentioned authors individual species can be tentatively grouped into one of three dietary adaptations. Large values indicate a substantial functional participation of the large intestine, small values a greater participation of small intestine in the absorptive process. A coarse ranking can be attempted based on these ratios such that all animals with values between 0–30 are classified as faunivores, 30–70 as intermediate feeders and above 70 as herbivores.

Also for volumes a favourable method to analyse volume data is to calculate ratios of: volume large intestine to volumes small intestine (× 10), giving a "Coefficient of Volume" (equivalent to "Coefficient of Fermentation" according to Chivers and Hladik 1980, 1984). Large values indicate a high participation of caecum and/or colon in the fermentation processes (tendency toward herbivory). In Table 3 ratios between 0–7 equal faunivores, 7–15 = intermediate feeders and above 15 = herbivores.

Table 3. **Coefficient of volume**

Presents the ratio of the volume of large intestine divided by the volume of the small intestine

F = Faunivore Rating: 0–7		I = Intermediate 7–15		H = Herbivore 15+	
Human	0.4	Mouse	7.2	Muskrat	27.5
Cow (R)	3.7	D. hamster	9.1	Horse	29.8
Dog	4.1	Vole	9.8	Guinea pig	31.7
Goat (R)	4.1	Gerbil	9.9	Rabbit	71.2
Sheep (R)	7	Pig	9.9		
		Rat	10.1		
		G. hamster	12.5		
		Mole rat	14.1		
		Nutria	14.3		

Large intestine = Caecum + Colon; all values × 10. R = Ruminant.

Area to unit volume relationships

The relation of area to volume is a biologically important and interesting aspect morphometrically. By dividing the area of an intestinal region by its volume the area (cm^2) per unit volume (ml) can give an estimate of the amount of surface area available for absorption. These have been calculated for both basal areas (all 18 species) as well as for total areas (11 species (Table 4). Higher values indicate an advantageous surface area to volume relationship such that absorption is enhanced due to a more auspicous opportunity for digestible material in the lumen to contact the mucosal wall. It is obvious in Table 4 that smaller animals have higher values, i.e., their area/volume relationships are more advantageous than for larger animals, perhaps in correlation to their higher metabolic requirements (slope of regression curves: small intestine −0.38; caecum −0.38; colon −0.28; total intestine −0.41) (graphs not shown).

Table 4. **Area (cm^2) to volume (ml)**

This factor was determined to express the amount of area available in the different compartments of the gut in relation to volume. The ratios were obtained by dividing area by volume. The animals are listed from the smallest to largest according to body weight. Both basal area/volume and total area/volume are given. Smaller animals have higher values, i. e., have a more advantageous relationship of area to volume

Animal	Small intestine		Caecum		Colon		Total intestine	
	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol
Vole	12.7	50.3	8.7	15.5	19.1	37.3	12.5	36.8
Dwarf hamster	10.8	28.8	6.3	9.8	13.3	17.3	10.1	21.3
Mouse	10.0	25.7	5.0	9.1	8.3	13.0	8.6	19.5
Gerbil	9.6	24.4	4.2	7.4	13.5	22.5	8.1	12.3
Mole rat	10.6	–	9.6	–	15.9	–	10.8	–
Golden hamster	6.6	25.5	3.9	6.7	9.0	11.8	6.2	16.1
Rat	9.9	22.6	2.9	4.6	8.4	13.9	7.1	14.6
Muskrat	4.6	12.9	1.7	4.3	5.6	11.9	3.0	7.6
Guinea pig	5.8	18.5	1.3	2.9	6.6	10.3	3.1	7.7
Rabbit	5.8	19.5	1.0	2.2	5.3	9.7	1.9	4.9
Nutria	4.1	15.2	1.3	2.4	3.7	7.7	2.8	8.4
Dog	3.0	–	1.7	–	2.1	–	2.7	–
Sheep	4.2	–	1.1	–	3.2	–	3.6	–
Goat	3.2	–	1.4	–	3.9	–	3.2	–
Human	0.6	2.0	0.8	1.5	1.6	3.9	0.6	2.1
Pig	2.3	–	0.8	–	1.4	–	1.8	–
Cow	1.9	–	0.9	–	1.6	–	1.8	–
Horse	0.9	–	0.2	–	0.3	–	0.4	–

Basal = Basal areas; Total = Total areas (Basal area × SEF)

Discussion

The present study has employed modern techniques of morphometry to obtain quantitative data from intestines of 18 mammalian species. The advantages of the present technique include determining the basal areas by measurement of the entire large intestine and not, as previously undertaken, to sample small regions of the large intestine and extrapolate these values to the total length of the large intestine or to determine areas according to formulas by measuring length and breadths (Chivers and Hladik 1980). A second advantage is the use of imagine analysis to determine microscopically visible surface enlargements, which until now have not be included in most studies of intestinal surface area determination.

To interpret morphometric data as a whole (Table 1) it appears expedient to use a linear regression analysis of the individual parameters plotted against metabolic body weight, which is allowed by the distribution of the values. In this way a trend for each aspect can be recognized with respect to differences in body weights. Since the alimentary canal is directly related to satisfying metabolic requirements of the animal, it appears appropriate to use metabolic body weights instead of absolute body weights (Schmidt-Nielsen 1975). By use of the regression lines each individual value can be viewed with respect to this best fitted line, which describes the y of the investigated system with increasing (metabolic) body weight. As mentioned by Martin et al. (1985; see also Stark et al. 1987) not only the trend itself is of biological significance but rather how closely the individual values fit to the line and the subsequent search for a biological significance when a value is distant from the regression line. This aspect will be taken up when such obviously deviant values appear.

Area

The parameter basal area increases with increasing metabolic weight (except caecum) but does not keep pace with an increase in absolute body weight. For the 11 species where histological material was available the basal areas were multiplied by their SEF. Here such important structural entities as villi and plicae circulares for surface enlargement in the small intestine, and mounds, plicae obliquae, folds and "opened crypts" in caecum or colon (Snipes 1978, 1979a, b, 1981, 1982, 1985; Snipes and Thiele 1989; Snipes et al. 1982, 1988, 1990) are taken into consideration. Heretofore, these aspects have been neglected by other investigators. The importance of this type of augmentation can be seen by comparing the basal values with total area values in Table 1. (See Snipes 1991 for a morphological study of these various anatomical structures.) The regression lines for total areas against metabolic body weight give similar slopes as for basal areas, although direct comparison is not warranted in so far as seven species are not considered in the total area analysis. To make a comparison, slopes were additionally calculated for "basal areas" from only the 11 species that were available for SEF analyses. Slopes for basal areas versus slopes for total areas for the 11 species differ only minimally (for small intestine, respectively, 0.97 vs 1.01; for caecum 0.74 vs 0.77; for colon 0.81 vs 0.89 and total intestine 0.94 vs 1.00).

In each case the regression line for total surface area is closer to isometry. The difference between the two regression lines expresses the degree to which these second-order micro-anatomical enlargements increase the surface area over and above the basal area. The intestinal values for area all show negative allometric scaling to absolute body weight as does metabolim, which surprisingly is in contrast to lung parameters, which scale isometrically with absolute body weight (Duncker 1989).

Volume

In the present study volumes were determined from measured basal areas and lengths. Volumes determined by filling with water or other material possess the inherent danger of stretching and over dilating the pliable intestinal walls (Chivers and Hladik 1980). In all cases, regression lines for small intestine, caecum, colon and total intestine (Figs. 5) indicate that volume scales positive allometrically with metabolic body weight (MBW). Thus, the increase in volume for each intestinal region increases slightly more than expected for the body size with increasing metabolic weight. All coefficients of correlation were significant at the 0.1 % level.

With respect to absolute body weight, as expected, all values scale somewhat lower. This is especially true for caecum where the volume versus absolute body weight scales negative allometrically. In this case this may be more in tune with an adaptive situation, and what could almost be expected for a portion of the intestine that is not necessarily tubular or cylindrical such as the other compartments (save stomach). A parallel increase in the caecum could lead to topographical problems in the abdomen in large animals. By close inspection of the graphs it is interesting to note those species divergent from the straight line; notably for caecum: horse, rabbit, nutria, guinea pig and muskrat, are all hindgut fermenters where a large caecum as fermentation vat could be expected; whilst ruminants such as cow, goat and sheep and faunivores (e.g., dog) or "omnivores" (e.g., human and pig) all lie below the line. In the former animals a large caecum for their dietary adaptation (forestomach fermentation) is not required (Ulyatt et al. 1975; Langer 1986; Hofmann 1989).

Coefficients

The convenient handling of empirical data by transforming to ratios (Tables 2–4) allows a certain ease in surveying the data as well as to discover certain relationships that are not

immediately evident with raw data. Thus, the Coefficient of Differentiation (ratio of area large intestine to area small intestine) gives an indication of surface enlargement to volume in the respective gut compartments of small intestine or large intestine. High values are indicative of a tendency toward herbivory (see Table 2). Based on these high values dwarf hamster, horse, vole, golden hamster, guinea pig, muskrat, mole rat and rabbit can be placed in the category of herbivory. This rating correlates well with a highly developed large intestine (caecum and/or colon) possessing well-differentiated internal structures in these species (Luppa 1961; Snipes 1978, 1979a, b, 1982; Snipes et al. 1990). It is interesting to note when comparing the ratios for basal areas to the ratios for total areas in each animal a lower coefficient is found for the latter. This results from the proportionally much larger microscopically visible surface enlargements in the small intestine (villi, plicae circulares) than found in the large intestine (compare also SEF values in Table 1). The total areas (basal × SEF) give a more realistic value for the situation in the gut. Basal areas are also given here since to our knowledge all comparative investigations to date have used only basal areas or their equivalents. Note that ruminant forms (sheep, goat, and cow) possess values in the faunivore or lower intermediate ranges. The role of the hindgut in ruminant digestion has been discussed by Janis (1976), Ulyatt et al. (1975) and Hofmann (1989).

The equivalent ratios for volumes (volume large intestine/volume small intestine) (Table 3) give a Coefficient of Volume and affords perhaps a better indication of herbivory than the previous coefficient for area. According to this criterion the following species qualify as herbivores: muskrat, horse, guinea pig and rabbit. This classification appears to be somewhat more restrictive. Note here that ruminants show lower values and range again with faunivores. Again this is not surprising since they possess a complicated and voluminous forestomach for their fermentation function.

The intermediate classification contains the largest number of animals. Nutria, golden hamster and mole rat border on values to herbivory and at least in the case of nutria and mole rat the dietary strategy and morphological aspects of the caecum are reminiscent of herbivory. The morphological aspects of the latter species' intestines speak for their inclusion in the category "herbivory" (nutria: Wagner 1963; Kämmerer and Wetzig 1966; Stahl 1987; Snipes et al. 1988; mole rat: Snipes et al. 1990). Borderline values such as these indicate that the classification should not be held rigid but rather should be looked upon as a continuum and as a dynamic concept. For want of a better designation, "intermediate" at least allows classifying animals with varied dietary types and it is preferable to the older term "omnivore". The rat (Sperber et al. 1983; Snipes 1981) (perhaps also pig) may be an example of a "true" omnivore. The other members of the intermediate group (especially gerbil, hamster, vole) often show changes in dietary habit in adaptation to seasonal, climatic, environmental and ambient conditions and are better placed in a neutral classification denominated "intermediate". Volume coefficients give a relatively good indication of the presence of a large fermentation vat in the hindgut (either caecum and/or colon) as substantiated by the well-known anatomy of the large intestine of horse (Chivers and Hladik 1980), rabbit (Snipes 1978), guinea-pig (Gorgas 1967; Snipes 1982) and muskrat (Luppas 1961).

Area to unit volumes

The area to volume ratios give an impression of the amount of area available within a compartment of the intestine in relation to its volume. Granted, large animals have greater intestines and therefore empirically more surface area, but relatively seen by use of this ratio the relationship changes to the advantage of the smaller animals.

In voluminous sacs such as large caeca in some herbivores the situation could tend to become disadvantageous for the contact of digesta with mucosal wall, unless a special anatomical adaptation is introduced to increase the area to volume relationship. In both the

rabbit (Snipes 1978) and mole rat (Snipes et al. 1990) a spiral fold courses throughout the entire caecum and increases the surface area several fold and thus enhances the contact possibility of intestinal wall and luminal content. This unit factor appears to be correlated more closely with body weight than with dietary type. It is obvious that small animals have more advantageous surface to volume relationships (Table 4). This could correlate with the higher metabolic rates in small animals and their correlative higher energy requirements which must be fulfilled by a more efficient absorption (possibly through advantageous surface to volume relationships).

By comparing the ratios gained for basal area/volume with values for total area/volume for each intestinal portion certain tendencies become apparent. The ratios increase from basal to total areas in all regions of the intestine as would be expected (that portion due to micro-anatomical enlargements) but to differing degrees. For example, the differences for small intestine are greater than for large intestine (caecum and colon). This evidently reflects the greater dimension due to villi in the small intestine compared to such enlargements in the large intestine (widened crypts, folds, mounds; Hladik 1967; Snipes 1991). These differences again reflect the amount of the SEF factor in each region. (See Table 1).

Studies are in progress to advance the morphometrical analysis to the ultrastructural level to account for the surface area enlargement due to microvilli.

Granted, many other factors also play decisive roles in the different dietary adaptations. One important aspect is the transit time of gut content through the intestine (Warner 1981; Langer 1991; Langer and Snipes 1991).

Another important factor when considering surface area relationships is the presence of the glycocalyx and the mucus layer covering the mucosa (Sakata and v. Engelhardt 1981). Moreover, the true diffusion factor of digestible material through the mucosal wall must take into consideration similar factors that have been determined for the lung (Duncker 1989), namely, an anatomical diffusion factor.

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Zusammenfassung

Quantitaive Untersuchung an Gesamtoberfläche und Volumen verschiedener Darmabschnitte von 18 Säugetierarten

Untersucht wurden morphologische Parameter des Dünn- und Dickdarms von 18 Säugetierarten. Eine neue Methode wird beschrieben, mit der mittels Planimetrie Gesamtoberflächen von Darmabschnitten bestimmt wurden. Zusätzlich wurde ein Computer-unterstütztes Programm benutzt, mit dem auf lichtmikroskopischem Niveau die Vergrößerung der Oberfläche der Darmschleimhaut bestimmt werden kann. Hiermit wird ein Oberflächenvergrößerungs-Faktor festgestellt, welcher, mit den planimetrisch ermittelten Werten multipliziert, den Gesamtwert der Oberflächenvergrößerung des jeweiligen Darmabschnitts angibt. Die Daten werden in Koordinatensystemen dargestellt und zur Berechnung linearer Regressionen verwendet. Die Ergebnisse zeigen sehr deutlich, daß die Binnenflächen des Dünndarms, des Colons und des Gesamtdarms nahezu isometrische Beziehungen zum metabolischen Körpergewicht zeigen, während das Cäcum negative allometrische Beziehungen aufweist.

Der Quotient aus Gesamtfläche und Volumen der betrachteten Darmabschnitte bietet eine Vorstellung über die Binnenfläche, die pro Volumeneinheit verfügbar ist. Kleinere Säuger haben pro Volumeneinheit eine relativ größere Binnenoberfläche als große. Dieser Befund wird auf die höhere Stoffwechselrate der kleineren Säuger zurückgeführt.

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